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# Permineralized Matoniaceous Fossils from the Cretaceous of Japan[1)]

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A fossil matoniaceous rhizome, *Tricyclopteris japonocretacea* gen. et sp. nov. is described from the Upper Cretaceous of Hokkaido, Japan. The rhizome has a tricyclic solenotele with endarch primary xylem. A matoniaceous petiole or rachis, *Matoniostipes mesozoica* Nishida (1973) from the Lower Cretaceous of Choshi, Chiba Prefecture, is emended and reexamined for comparison. It has loose parenchyma (Seward 1899) near protoxylem like the petiole of living *Matonia pectinata. Matonia pectinata* is also characterized by a small cavity parenchyma (Holder, 1925: Ogura, 1972) near protoxylem in the rhizome, while it does not occur in *Tricyclopteris.*

(Continued from Yoshida et al., Res. Inst. Evolut. Biol. Sci. Rep. **8**: 85–94, 1996)

## Introduction

The Matoniaceae is a rather small family of leptosporangiate fern. The family consists of two living genera *Matonia* (2 spp.) and *Phanerosorus* (1 sp.). The species are restricted to the paleotropical regions and prefer habitat in forest floor or margin, though it is well known from the fossil records that the family was cosmopolitan during the Mesozoic.

Fossils that are comparable to the Matoniaceae are being found ever since the Triassic. Impression or compression fossils such as *Phlebopteris* Brongniart (1836) (= *Laccopteris* Presl 1838) (the Upper Triassic to the Cretaceous) and *Matonidium* Schenk (1871) (Jurassic and Cretaceous) have shown worldwide distribution. *Delosorus* Skog (1988) is an American foliage genus from the Lower Cretaceous. These are all impression or compression foliage. The first record of permineralized matoniaceous rhizome is based on a badly preserved specimen from the Jurassic of India (Sharma and Bohra 1978).

Tidwell and Skog (1992) described two genera of different ages from Tasmania. Mid-Mesozoic *Tasmanopteris* has a polycyclic siphonostele and Tertiary *Heweria* has similar structure. However, Tidwell and Skog (1992) state possible Mesozoic origin of *Heweria.*

*Matoniostipes mesozoica* (Nishida 1973) is the first record of permineralized matoniaceous fossil in the world from the Lower Cretaceous of Chiba Prefecture, Japan. It is emended by reexaminations of type specimen. The fossil which will be described here is a fern rhizome collected by the first and third authors from the Upper Cretaceous of Yubari City, Hokkaido. It has a tricyclic stele characteristic of a matoniaceous rhizome. The rhizome is compared to the early described fossils and living *Matonia*, and is designated here as a new genus of the Matoniaceae.

## Materials and Methods

Specimen No. 82301 is a permineralized fern rhizome 6 mm long and 4 mm in diameter, with fairly well preserved histology. It is cylindrical in original shape, but one-third of it is degenerated or lost during the diagenesis. The specimen is embedded in a calcareous nodule found from the riverbed of the Yubari River, along downstream from Hakobuchi dam, Ohyubari, Yubari City, Hokkaido, Japan. The nodule containing the fossil also include marine fauna and shows lithological features of the nodules derived from the Upper Cretaceous Middle or Upper Yezo Group (Turonian-Santonian), which are widely distributed along the Yubari River. A cyatheaceous tree fern petiole, *Thyrsopterorachis* (H. Nishida and Nishida 1979) has been described from the same area. Geological information should be referred to the previous paper (H. Nishida and Nishida 1979). Micropreparations were made by ordinary peel method (Joy et al. 1956) using 1.8% hydrochloric acid as an etching reagent.

We used micropreparations of *Matonia pectinata* made by the late Prof. P. Maheshwari, India, for comparison.

Micropreparations of the type specimen of *Matoniostipes* being deposited at Chiba University were compared to the fossil rhizome.

## Results

Taxonomic treatment

Class Filicopsida

Order Filices Leptosporangiatae

Family Matoniaceae C. Presl (1847)

Genus **Tricyclopteris** H. Nishida, A. Yoshida & Nishida, **gen. nov.**

Type species. *T. japonocretacea* H. Nishida, A. Yoshida & Nishida sp. nov. (Figs. 2–6).

Diagnosis of the genus. Permineralized fern rhizome with tricyclic stele; outer and middle stelar rings amphiphloic and with chiefly endarch or a few mesarch xylem; innermost stele ectophloic centrarch protostele; xylem consisting of scalariform tracheids and xylem parenchyma, lacking cavity parenchyma near protoxylem. Each stele surrounded by sclerenchyma tissue consisting of thick-walled cells.

Etymology. The genus name originates from the tricyclic stele of rhizome.

**Tricyclopteris japonocretacea** H. Nishida, A. Yoshida & Nishida, **sp. nov.**

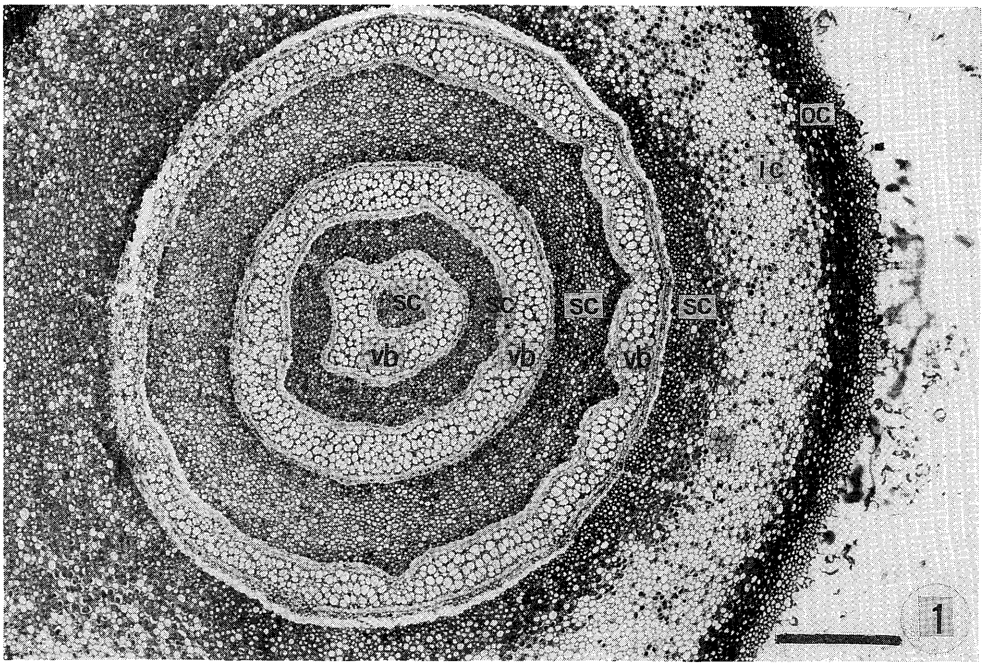
Species diagnosis. As that of the genus.

Etymology. The specific epithet means the fossil occurrence (Japan) and age (Cretaceous).

Deposition. Micropreparations of the holotype specimen (No. 82301) is housed in the Laboratory of Phylogenetic Botany, Faculty of Science, Chiba University, Japan.

Description. Rhizome cylindrical, without prominent dorsiventrality, 4.0 mm in diameter and with tricyclic stele. The outer and middle steles amphiphloic solenostele, and the inner a protostele (Fig. 2). Epidermis eroded and lost. Hypodermal layer consists of sclerenchyma of 2–3 cells thick; cells rectangular in cross section, 12.5–25 $\mu$m in diameter. Outer cortex 3–5 cells wide, composed of thick-walled parenchyma, while inner cortex 7–10 cells wide, composed of thin-walled cells; cells 65–75 $\mu$m in diameter (Fig. 2). Each stelar ring surrounded by a sclerenchyma sheath of 5–7 cells thick. The sclerenchyma cells 25–37.5 $\mu$m in diameter (Figs. 3, 4 and 6). Endodermis mostly degraded. Diameter of stelar rings 2.0 mm in the outer, 0.9–1.0 mm in the middle and 0.2 mm in the central protostele. In the external stelar ring, the xylem plate slightly undulates in the inner contour (Fig. 2, between arrows). The xylem chiefly endarch or rarely mesarch with ca. 15 protoxylem points. Metaxylem tracheids have scalariform wall thickening. The most part of phloem degenerated. Xylem mass of the central protostele centrarch and consists of less than 10 cells (Fig. 4). Cavity parenchyma absent near protoxylem (Fig. 5).

Affinity. the slender elongated rhizome with



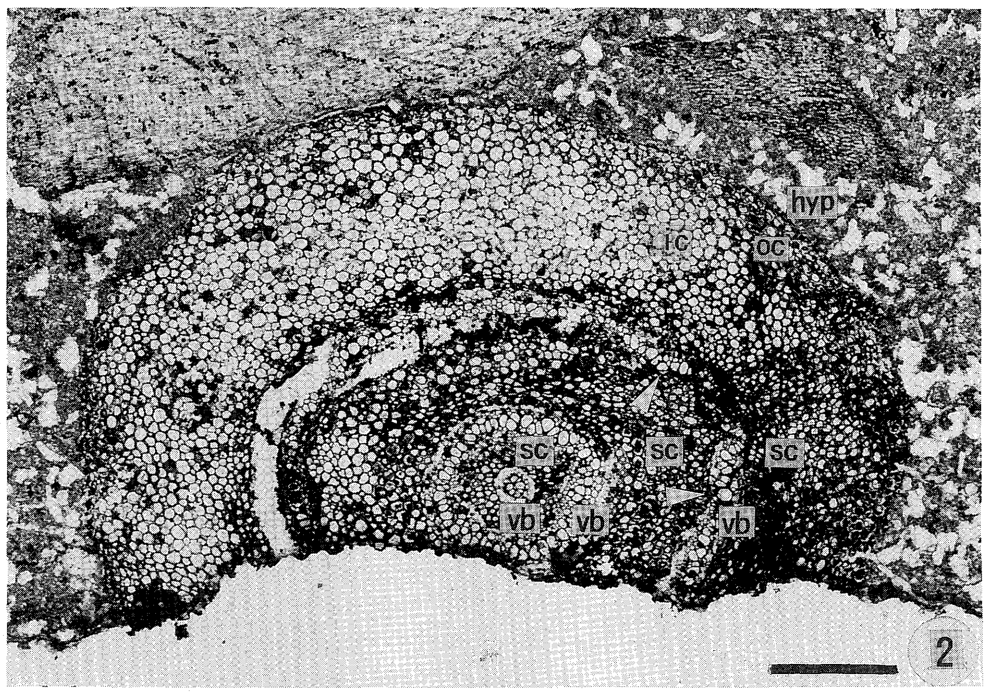
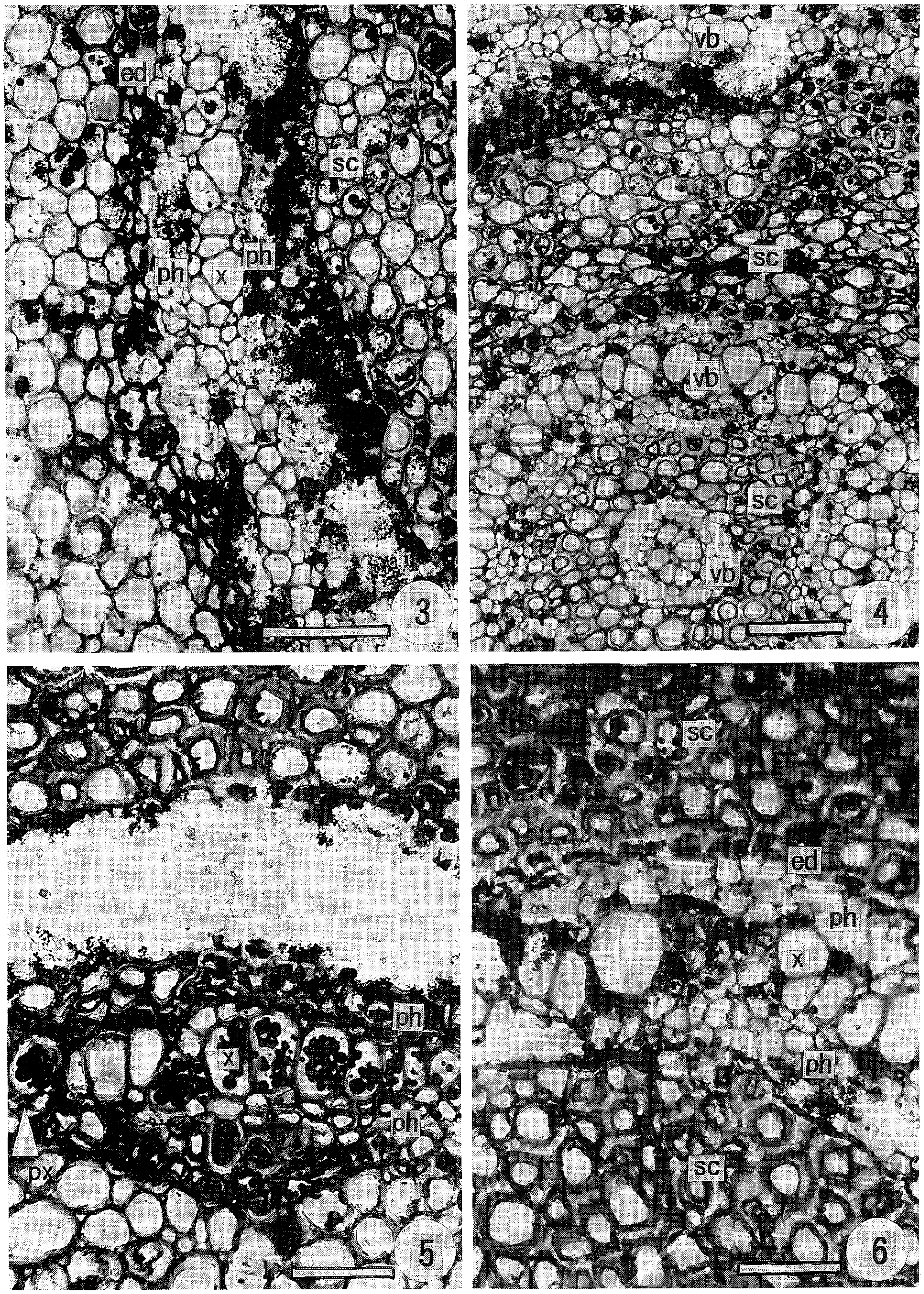




Fig. 1. Cross section of rhizome of living *Matonia pectinata* showing tricyclic solenostele. Each stelar ring is surrounded by sclerenchyma sheath. Inner contour of the outer ring undulate. Upper side of rhizome to the right. Scale bar: 1 mm. Fig. 2. Cross section of rhizome of *Tricyclopteris japonocretacea* gen. et sp. nov., showing tricyclic stele, sclerenchyma sheath, and xylem plate folding (between two arrowheads). Scale bar: 0.5 mm.

Abbreviations. Ab: abaxial side, Ad: adaxial side, ed: endodermis, oc: outer cortex, p: parenchyma, ph: phloem, px: protoxylem, sc: sclerenchyma sheath, vb: vascular bundle, x: xylem.




Figs. 3–6. *Tricyclopteris japonomesozoica* gen. et sp. nov. Fig. 3. Part of outer stelar ring, showing amphiphloic concentric bundle with endarch xylem and surrounding sclerenchyma sheath. Scale bar: 100 $\mu$m. Fig. 4. Stelar rings enlarged. Scale bar: 100 $\mu$m. Fig. 5. Outer stelar ring enlarged, showing absence of cavity parenchyma near protoxylem. Scale bar: 50 $\mu$m. Fig. 6. Part of middle stelar ring enlarged. Scale bar: 50 $\mu$m.

tricyclic stele structurally characterizes *Tricyclopteris*. The amphiphloic concentric bundles and xylem maturation, which is chiefly endarch or rarely mesarch, are also characteristic features. The stelar configuration and presence of endodermis attribute the *Tricyclopteris* to leptosporangiate ferns. In the living leptosporangiate ferns, a polycyclic stele occurs in *Acrostichum*, *Dennstaedtia*, *Matonia*, *Pteris*, *Saccoloma*, and *Thyrsopteris* (Bower 1918, 1926, 1928; Ogura 1972). *Acrostichum*, *Saccoloma* and *Thyrsopteris* differ from *Tricyclopteris* in having nests of medullary bundles in the pith. The vascular cylinder of Pteridaceous ferns such as *Pteris* and *Dennstaedtia* shows polycyclosteley with variable thickness; usually thicker on dorsal side and resulting in a slight dorsiventrality of the rhizome anatomy.

A tricyclic stele similar to *Tricyclopteris* is reported in *Pteris podophylla* Swartz of the Pteridaceae (Troop and Mickel 1968). Although the specimen of *P. podophylla* is not available to us, the general structure of *Tricyclopteris* does not fit that of *Pteris*. The outer ring of polycyclostely in the pteridoid ferns is distorted in configuration (Bower 1923), unlike a complete circle of *Tricyclopteris* and *Matonia*.

*Tricyclopteris* rhizome is slender in compared to that of *Matonia pectinata*. Thinner xylem plate of *Tricyclopteris* is probably due to the size difference. Though the innermost stele is solenostelic in mature *M. pectinata*, it is protostelic like *Tricyclopteris* in a slender rhizome (Tansley and Lulham 1902, 1905). In *M. pectinata*, the dorsal side of the external vascular cylinder is undulated especially along its inner contour. This undulation corresponds to that more characteristically expressed in the inner contour of petiole vascular bundle. In *Tricyclopteris*, the inner contour of the outer vascular cylinder does not undulate significantly, however, the xylem plate is folded in some parts (Fig. 2, between arrowheads).

The slender rhizome of *Tricyclopteris* resembles that of *Phanerosorus* which is 3 mm in diameter, while *Matonia* rhizomes range from 9 to 10 mm in diameter. However, the stele of *Phanerosorus* is dicyclic.

*Matonia* rhizome is characteristic in having cavity parenchyma near protoxylem (Holder 1925) (Figs. 7 and 8). Such cavity parenchyma is absent in *Tricyclopteris* (Fig. 5).

Sharma and Bohra (1978) reported a *Matonia*-like silicified rhizome with tricyclic stele from the Jurassic of Rajmahal Hills, India. It is 0.9–1.2 cm in diameter and is thicker than *Tricyclopteris*. The three stelar rings are amphiphloic having mesarch xylem plate instead of chiefly endarch one in *Tricyclopteris*. The xylem plate is 3–5 cells thick instead of 1–3 in *Tricyclopteris*.

*Matonidium* sp. from Belgium Wealden (Seward 1910) is a permineralized rhizome with poorly preserved internal structure and cannot be compared to *Tricyclopteris*.

Tidwell and Skog (1992) described two matoniaceous genera, *Tasmanopteris* and *Heweria* from Tasmania, Australia. Although *Heweria* is found from the Tertiary sediments, its preservation type and possible reworked nature suggested the Mesozoic origin (Tidwell and Skog 1992). *Heweria* resembles *Matonia* in having uniseriate, multicellular epidermal hairs. The tri- to hexacyclic stele of *Heweria* differs from tricyclic stele of *Matonia* and *Tricyclopteris*.

*Tasmanopteris* is characteristic in having mucilage canals in cortex, which are absent in *Heweria* and *Matonia*. *Tricyclopteris* also lacks mucilage canals in the cortex. Three Mesozoic genera, *Heweria*, *Tasmanopteris* and *Tricyclopteris* differ from *Matonia* in the absence of cavity parenchyma near protoxylem.

Tidwell and Skog (1992) reported exarch xylem maturation for living *Matonia* and two fossil genera they described. However, we

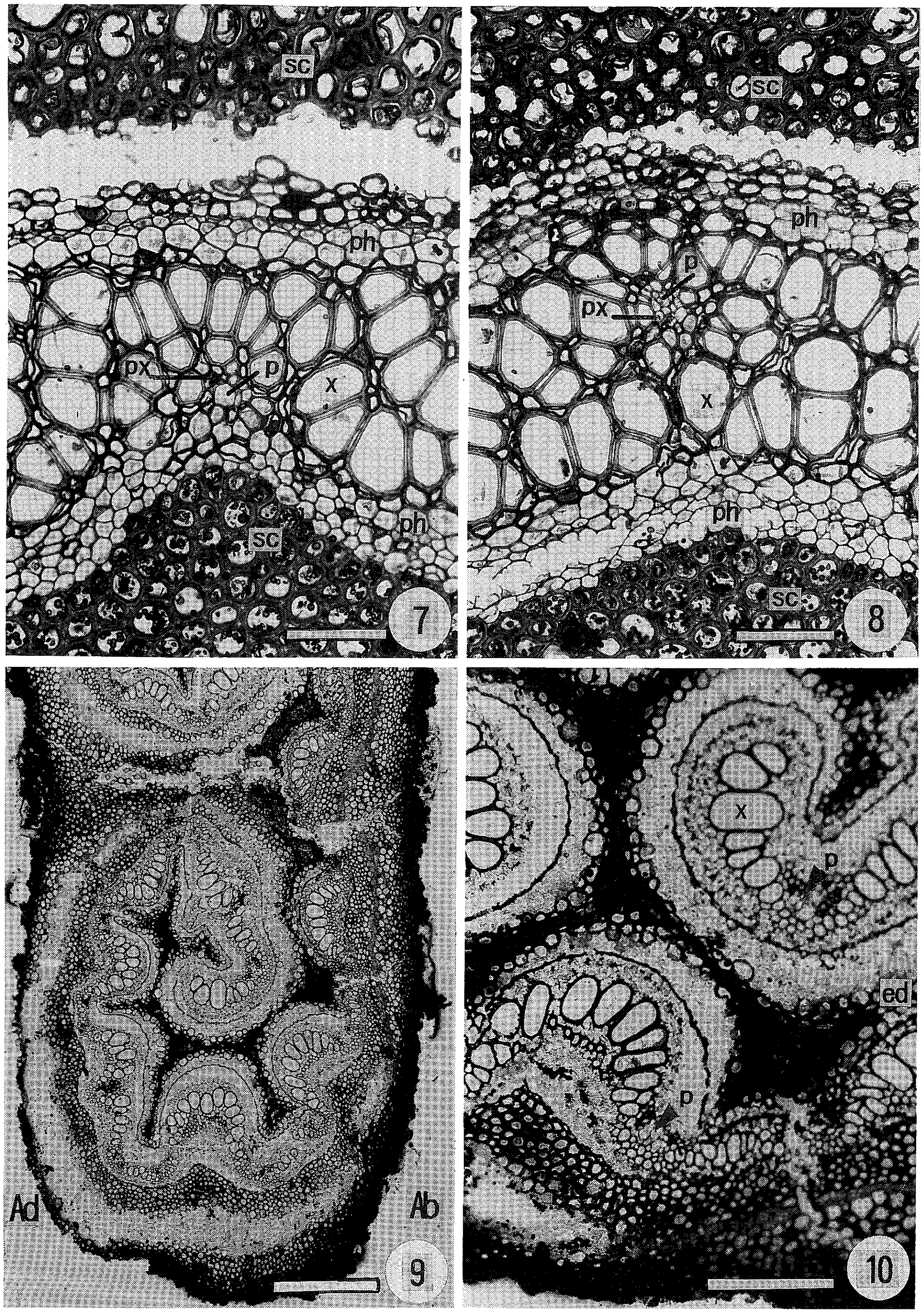



Fig. 7, 8. Magnified cross section of *Matonia pectinata* rhizome, showing endarch to mesarch xylem, and protoxylem areas accompanied with cavity parenchyma. Scale bar: 100 $\mu$m. Figs. 9, 10. *Matoniostipes mesozoica* Nishida. Fig. 9. Half of cross section of the specimen, showing C-shaped vascular bundle with deeply incurved adaxial ends. Scale bar: 500 $\mu$m. Fig. 10. Enlarged vascular bundle, showing parenchyma cells near protoxylem areas. Scale bar: 250 $\mu$m.

could not confirm any exarch xylem in *Matonia* we have examined, nor in *Tricyclopteris* (Figs. 2 and 3).

**Matoniostipes mesozoica** Nishida in Bot. Mag. Tokyo **86**: 189 (1973).

Emended description. Permineralized fern petiole or rachis with matoniaceous vascular arrangement. Vascular bundle C-shaped with deeply incurved adaxial ends in cross section; inner contour strongly undulate. Protoxylem present at inner corner of each constriction. Loose parenchyma present on inner side of each protoxylem. Vascular bundle surrounded by thin sclerenchyma sheath; sclerotic cells 15–35 $\mu$m in diameter. Hypodermal tissue consists of several layers of thick-walled cells, 8–12 $\mu$m in diameter. Outer cortical tissue consists of large parenchyma cells, 28–45 $\mu$m in diameter, smaller toward vascular bundle. Convex part of wavy xylem plate 10–15 tracheids thick; tracheids ovoid or cocoon-shaped in cross section, 38–75 $\mu$m in short and 55–140 $\mu$m in long diameters.

Affinity. *Matoniostipes mesozoica* is a fern petiole or rachis having a vascular arrangement of *Matonia*-type (Ogura 1938, 1972); a continuous C-shaped configuration with deeply incurved adaxial ends. Its xylem plate is flat along the external side, but the inner side is highly corrugated. Another feature of *Matoniostipes* is a loose parenchyma mass associated with protoxylem, which is also present in the petiole of *Matonia pectinata* (Seward 1899). Such parenchyma occurs in the outer ring of tricycle stele in the rhizome of *Matonia pectinata.* This parenchyma is similar to the protoxylem cavity parenchyma which was found by Holden (1925) in the rhizome of *M. pectinata.* As the loose parenchyma was overlooked in the original description (Nishida 1973), we emend here the diagnosis of *Matoniostipes. Matoniostipes*, however, differs from *Matonia* in lacking mucilage canals in the cortex which are present in *Matonia* (Ogura 1972).

Discussion. From the Upper Cretaceous of Hokkaido, a large number of permineralized fern fragments belonging to a diverse array of genera and families have been described since Stopes and Fujii (1910) first described schizaeaceous fertile pinnule, *Schizaeopteris*, and a fragment of cyatheaceous tree-fern midrib, *Fasciostelopteris*, from Ohyubari, Hokkaido. According to Nishida (1991) the following genera are known to date: *Cyathocaulis* Ogura, *Cyathorachis* Ogura, *Loxsomopteris* Skog, *Paracyathocaulis* H. Nishida, *Solenostelopteris* Kershaw, *Thyrsopterorachis* H. Nishida & Nishida, and *Yezopteris* Ogura. Nishida (1991) also listed preliminarily a dennstaedtioid petiole or rachis, and a gleichenioid petiole.

Except for *Loxsomopteris* (Loxsomaceae) and *Solenostelopteris* (family *incertae sedis*), most genera above belong to the Cyatheaceae in a broad sense. *Schizaeopteris* has been compared to the extant genus *Anemia* of the Schizaeaceae since it was first described by Stopes and Fujii (1910). Yoshida et al. (1996b) confirmed this affinity based on spore morphology. Recently an *Osmundites* petiole (Osmundaceae) was added to the Hokkaido Cretaceous flora (Yoshida et al. 1996a). *Tricyclopteris* is a representative of the Matoniaceae new to the flora.

The Matoniaceae is known to have had a world-wide distribution throughout the Mesozoic, beginning with the Upper Triassic foliage *Phlebopteris* followed by *Matonidium, Nathorstia*, etc. The permineralized specimens known to date; *Matoniostipes mesozoica* Nishida (1973), a matoniaceous rhizome (Sharma and Bohra 1978), *Tasmanopteris richmondii* Tidwell & Skog (1992), *Heweria kempii* Tidwell & Skog (1992) and *Tricyclopteris japonocretacea* H. Nishida et al. (present paper) show similar distributional

pattern to that inferred from the foliage record.

Structurally, *Matoniostipes* closely resembles *Matonia* in having loose parenchyma near protoxylem, but differs from the latter in lacking mucilage canals in the cortex. Among four rhizomes, *Heweria* most resembles *Matonia* in having epidermal attenuate hairs.

One of the largest relatives of the family is *Weichselia* (Stiehler 1857) attaining to a considerable size. *Weichselia* has a massive stem bearing helically arranged large fronds with thick petioles, 5 cm in diameter. The permineralized petiole of *Weichselia* is known as *Paradoxopteris* (Edwards 1933, Alvin 1971) having up to 12 rings of vascular bundles. Besides many similarities, *Weichselia* differs from the Matoniaceae in having non-laminar fertile pinnules, polycyclic petiole traces, bipinnately compound leaves, and different arrangement of soral sporangia (Alvin 1968, 1971; Taylor and Taylor 1993) and is sometimes treated as a separate family Weichseliaceae (Alvin 1971).

We wish to express our hearty thanks to Dr. Yasuji Fukuda, Principal of Musashi High School, for his adequate suggestion to the histology of the fossil. Gratefulness is also due to the staff of the Laboratory of Phylogenetic Botany, Faculty of Science, Chiba University for granting us permission to use laboratory facilities.

## Endnote

[1]Structure and affinities of the petrified plants from the Cretaceous of Northern Japan and Saghalien 24. Contributions from the Research Institute of Evolutionary Biology, No. 117. Supported by a Grant-in-Aid for Scientific Research from the Ministry of Education, Science, Literature and Sports to H. N.

### References

Alvin K. L. 1968. The spore-bearing organs of the Cretaceous fern *Weichselia* Stiehler. J. Linn. Soc. (Bot.) **61**: 87–92.

——— 1971. *Weichselia reticulata* (Stokes et Webb) Fontaine from the Wealden of Belgium. Mem. Inst. Roy. Soc. Nat. Belgique **166**: 1–33.

Bower F. O. 1918. Studies in the phylogeny of the Filicales VII. Pteroideae. Ann. Bot. **32**: 1–68.

——— 1923. The Ferns. I. Cambridge University Press, Cambridge. 359 pp.

——— 1926. The Ferns. II. Cambridge University Press, Cambridge. 344 pp.

——— 1928. The Ferns. III. Cambridge University Press, Cambridge. 360 pp.

Brongniart A. 1836. Histoire des végétaux fossiles; ou recherches botaniques et géologiques sur les végétaux renfermés dans les diverges couches du globe: vol. **1**: 369–488.

Edwards W. N. 1933. On the Cretaceous fern *Paradoxopteris*, and its connexion with *Weichselia*. Ann. Bot. **47**: 317–341, pls. 14.

Holden H. S. 1925. On the occurrence of cavity parenchyma and tyloses in ferns. J. Linn. Soc. London **47**: 141–153.

Joy K. W., Willis A. J. and Lacey W. S. 1956. A rapid cellulose peel technique in palaeobotany. Ann. Bot. **20**: 635–637.

Nishida H. 1991. Diversity and significance of late Cretaceous permineralized plant remains from Hokkaido, Japan. Bot. Mag. Tokyo **104**: 253–273.

——— and M. Nishida. 1979. *Thyrsopterorachis*, gen. nov., a tree fern rachis from the Upper Cretaceous of Hokkaido, Japan. Bot. Mag. Tokyo **92**: 187–195.

Nishida M. 1973. On some petrified plants from the Cretaceous of Choshi, Chiba Prefecture VI. Bot. Mag. Tokyo **86**: 189–202.

Ogura Y. 1938. Anatomie der Vegetationsorgane der Pteridophyten. Handb. d. Pflanzenanat. I. Abt. I. 7, Teil. 2. Gustav Fischer, Berlin. 476 pp.

——— 1972. Comparative anatomy of vegetative organs of the Pteridophytes. Gebrüder Borntraeger, Berlin. 502 pp.

Presl C. 1838. *Laccopteris*. *In*: Sternberg G. K. (Ed.) Versuch einer Geognostischen Botanischen Darstellung der Flora der Vorwelt: **II (7–8)**: 81–220. Leipzich.

Schenk A. 1871. Beiträge zur Flora der Vorvelt. IV. Die Flora der nordwestdeutschen Wealdenformation. Palaeontogr. **19**: 203–262, pls. 22–43.

Seward A. C. 1899. On the structure and affinities of *Matonia pectinata*, R. Br., with notes on the geological history of the Matoniaceae. Phil. Trans. Roy. Soc. London, Ser. B. **191**: 171–209, pls. 17–20.

——— 1910. Fossil plants II. 624 pp. Cambridge Univ. Pr., London.

Sharma B. D. and Bohra D. R. 1978. A petrified matoniaceous rhizome from Amarjola in the Rajmahal Hills, India. Palaeobotanist **28**: 457–460.

Skog J. E. 1988. Reassignment of *Aspidium heterophyllum* to a new genus in the family Matoniaceae. Amer. J. Bot. **75**: 1120–1129.

Stiehler A. W. 1857. Beiträge zur Kenntniss der vorweltlichen Flora des Kreidegebirges im Harze. Palaeontogr. **5**: 47–70, 4 pls.

Stopes M. C. and Fujii K. 1910. Studies on the structure and affinities of Cretaceous plants. Philos. Trans. Roy. Soc. London Ser. B **210**: 1–90.

Tansley A. G. and Lulham R. B. 1902. On a new type of fern-stele, and its probable phylogenetic relations. Ann. Bot. **16**: 157–164.

——— and ——— 1905. A study of the vascular system of *Matonia pectinata*. Ann. Bot. **19**: 475–519, 3 pls.

Taylor T. N. and Taylor E. L. 1993. The Biology and Evolution of Fossil Plants. Prentice hall, Englewood Cliffs. 982 pp.

Tidwell W. D. and Skog, J. E. 1992. Two new fossil matoniaceous stem genera from Australia. Rev. Palaeobot. Palynol. **70**: 263–277.

Troop J. E. and Mickel J. T. 1968. Petiolar shoots in the Dennstaedtiaceae and related ferns. Amer. Fern J. **58**: 64–70.

Yoshida A., Nishida M. and Nishida H. 1996a. A permineralized Osmundaceous petiole from the Upper Cretaceous of Hokkaido, Japan. Res. Inst. Evolut. Biolog. Sci. Rep. **8**: 49–56.

———, Nishida H. and Nishida M. 1996b. Permineralized schizaeaceous fertile pinnules from the Upper Cretaceous of Hokkaido, Japan. I. *Schizaeopteris*. Res. Inst. Evolut. Biol. Sci. Rep. **8**: 85–94.

西田治文[a]，吉田　彰[b]，西田　誠[b]：**日本の白亜系産マトニア科鉱化化石**

北海道夕張市大夕張の夕張川川床から採集された上部白亜系エゾ層群に由来するノジュール中から見つかった根茎鉱化化石をマトニア化の新属・新種，*Trycyclopteris japonocretacea*として記載した．この根茎化石は細く，内皮を伴う3重の同心円状の維管束を持つ．外側の維管束は完全な環状，髄内維管束群を欠く，維管束環に背腹性がない，などの点でマトニア科と見なされる．外側の二つの維管束環は両師型の環状中心柱で，木部は主として内原型，中央のものは原生中心柱である．外側の維管束環は内側がやや波状となり，約15の原生木部を持つ．原生木部の内側に柔組織を伴わない．比較のため観察を行った現生の*Matonia pectinata*の葉柄には原生木部内側に柔組織が観察された．この組織はSeward（1899）がloose parenchymaとして報告しているが，同様の組織が千葉県銚子市の下部白亜系産マトニア科葉柄化石*Matoniostipes mesozoica* Nishida（1973）にも見られた．Holden（1925）はこれに似た柔組織を*Matonia pectinata*の根茎に見出しており，根茎と葉柄の柔組織はお互いに関連があると考えられる．この柔組織は*Matoniostipes mesozoica*を特徴づけるので，同種の記載を改訂した．

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